Psychoneuroendocrinology 72 (2016) 182–189

Contents lists available at ScienceDirect

Psychoneuroendocrinology

journal homepage: www.elsevier.com/locate/psyneuen

Influence of oxytocin on emotion recognition from body language: A randomized placebo-controlled trial

Sylvie Bernaerts[a,*], Emmely Berra[a], Nicole Wenderoth[b], Kaat Alaerts[a]

[a] Research Group for Neuromotor Rehabilitation, Department of Rehabilitation Sciences, KU Leuven, Leuven, Belgium
[b] Neural Control of Movement Lab, Institute of Human Movement Sciences and Sport, Department of Health Sciences and Technology, ETH Zürich, Zürich, Switzerland

ARTICLE INFO

Article history:
Received 21 March 2016
Received in revised form 9 June 2016
Accepted 4 July 2016

Keywords:
Oxytocin
Emotion recognition
Point light displays
Biological motion
Mirror system

ABSTRACT

The neuropeptide 'oxytocin' (OT) is known to play a pivotal role in a variety of complex social behaviors by promoting a prosocial attitude and interpersonal bonding. One mechanism by which OT is hypothesized to promote prosocial behavior is by enhancing the processing of socially relevant information from the environment. With the present study, we explored to what extent OT can alter the 'reading' of emotional body language as presented by impoverished biological motion point light displays (PLDs). To do so, a double-blind between-subjects randomized placebo-controlled trial was conducted, assessing performance on a bodily emotion recognition task in healthy adult males before and after a single-dose of intranasal OT (24 IU). Overall, a single-dose of OT administration had a significant effect of medium size on emotion recognition from body language. OT-induced improvements in emotion recognition were not differentially modulated by the emotional valence of the presented stimuli (positive versus negative) and also, the overall tendency to label an observed emotional state as 'happy' (positive) or 'angry' (negative) was not modified by the administration of OT. Albeit moderate, the present findings of OT-induced improvements in bodily emotion recognition from whole-body PLD provide further support for a link between OT and the processing of socio-communicative cues originating from the body of others.

1. Introduction

The neuropeptide 'oxytocin' (OT) is a nonapeptide produced by the paraventricular and supraoptic nuclei of the hypothalamus and is known to play a pivotal role in a variety of complex social behaviors. Initial animal and human research mostly focused on exploring the function of OT in childbirth, lactation and mother-child bonding (Galbally et al., 2011; Insel, 2010; Kendrick, 2000; Sue Carter, 1998), but more recently, accumulating evidence also demonstrated a strong involvement of OT in promoting prosocial behavior (Guastella and MacLeod, 2012), interpersonal bonding (Hurlemann and Scheele, 2015) and trust in adult relationships (Nave et al., 2015). One mechanism by which OT is hypothesized to promote prosocial behavior is by enhancing the processing of socially relevant information from the environment (Guastella and MacLeod, 2012). Increasing evidence suggests that exogenous OT can mediate the processing of emotional and socially relevant information, such as emotional faces and facial expressions (Domes, 2007; Schulze et al., 2011). Particularly, a single-dose of intranasally administered OT has been shown to enhance the detection of briefly presented facial expressions (Schulze et al., 2011) as well as the ability to accurately identify positive emotional facial expressions (Marsh et al., 2010). Exogenously administered OT has also been shown to stimulate gaze towards the eye region (Gamer et al., 2010; Guastella et al., 2008) and increase eye contact (Auyeung et al., 2015).

However, facial expressions are not the only source for conveying emotional and socially relevant information. In everyday life, the processing of other sources of socially-relevant information – such as the communicator's body language or 'bodily kinematics' – may be equally important for stimulating interpersonal social cognitive processes (Troje and Westhoff, 2006). To date however, only a handful of studies explored the effects of exogenously administered OT on the processing of biological motion originating from the body and bodily kinematics of others. One study by Kéri and Benedek (2009) used point light displays (PLDs) in which biological motion is presented by only a few moving dots that correspond to the movement of the body's main joints. Although highly impoverished in

* Corresponding author.
E-mail addresses: sylvie.bernaerts@kuleuven.be (S. Bernaerts), emmely.berra@student.kuleuven.be (E. Berra), nicole.wenderoth@hest.ethz.ch (N. Wenderoth), kaat.alaerts@faber.kuleuven.be (K. Alaerts).

http://dx.doi.org/10.1016/j.psyneuen.2016.07.002

terms of detail and background information, PLDs can readily evoke a vivid representation of a person. Interestingly, Kéri and Benedek (2009) showed for the first time that intranasal administration of OT can enhance the detection of biological motion PLD dots among a cloud of noise (mask) dots. Perry et al. (2010) extended this work by showing that intranasal OT can significantly enhance the extent of EEG mu suppression over the sensory-motor regions in the brain during the observation of PLD biological motion. Since mu suppression is considered a strong indicator of the extent by which observed actions are mapped or 'mirrored' onto the observer's own motor system, the results of Perry et al. (2010) provided initial neurophysiological evidence that OT can stimulate the processing of biological motion in the brain by altering 'mirror' motor resonance. Related to these findings, a more recent fMRI study provided indications that OT can alter the neural 'mirroring' of pain experienced by others (Bos et al., 2015). Interestingly, Bos et al. (2015) showed that a single-dose of OT significantly decreased neural activations in the insula and sensorimotor regions during the observation of painful stimuli experienced by others, which likely relates to the pain-reducing properties of OT. Aside the exploration of the effects of exogenously administered OT, Strauss et al. (2015) assessed levels of endogenous OT in blood plasma of patients with schizophrenia and showed that individual differences in plasma OT were associated with the 'reading of bodily expressions' (Strauss et al., 2015). Together, these studies provide strong indications of a link between OT and the processing of socio-communicative cues originating from the body of others.

To the best of our knowledge however, no studies to date directly investigated the effects of exogenously administered OT on the processing of emotional content embedded in biological motion kinematics or body language. To date, research mainly focused on exploring the effects of OT on emotion recognition from facial expressions. However, considering that bodily kinematics may provide subtle, but salient cues on the emotional state of others, it would be interesting to explore whether OT can affect this process.

In the present study, a double-blind between-subjects randomized placebo-controlled trial was conducted to specifically explore the effects of a single-dose of OT on the 'reading' of *emotional body language* as presented in impoverished biological motion PLDs. To this end, a bodily emotion recognition task was adopted in which participants had to indicate the emotional state of a whole-body PLD figure before and after a single-dose of intranasal OT.

2. Materials and methods

2.1. Study design

A randomized, double-blind, placebo-controlled, between-subjects design was used to test single-dose effects of intranasal oxytocin (OT) administration. Written informed consent was obtained from all participants prior to the study. Consent forms and study design were approved by the local Ethics Committee for Biomedical Research at the University of Leuven, KU Leuven (S56327) in accordance to The Code of Ethics of the World Medical Association (Declaration of Helsinki). The trial was registered with the European Clinical Trial Registry (Eudract 2014-000586-45) and the Belgian Federal Agency for Medicines and Health products.

2.2. Participants

A total of 46 healthy young adult men (23 OT, mean age = 21.50, S.D. = 2.02; 23 Placebo (PL), mean age = 21.78, S.D. = 2.11) were recruited to participate in the present study exploring single-dose effects of OT on the recognition of emotional states from point light displays (PLDs). Data from three participants (2 OT, 1 PL) were excluded from the analysis due to technical problems during data collection. All participants were recruited through advertisement within the university, such that approximately 90% of the included sample were university students. Participants were randomly allocated to receive OT or placebo (PL) nasal sprays. All participants were right-handed (self-reported) and mean age did not differ between OT and PL groups in both experiments. Only male participants were recruited to avoid potential sex differences in OT response as well as the potential interaction with the female hormonal cycle. Exclusion criteria were (i) age below 18 or above 30 years old (ii) a diagnosed psychiatric or neurological disorder, (iii) intake of psychotropic medication, (iv) history of neurological disease, and (v) history or evidence of other diseases (cancer, hematologic illness, endocrine disease, cardiovascular disease, respiratory condition, renal disease, liver condition or gastrointestinal illness).

The sample size of the current study exploring the effect of OT on the recognition of emotional states from PLDs was similar to the included sample size of a related study exploring the effect of a single-dose of OT on biological motion perception from PLDs (Kéri and Benedek, 2009). In this study, a within-subject design with a sample of 20 participants was adopted and a large effect of OT (versus PL) was revealed on improving the recognition of biological motion (versus recognizing non-biological motion) (Kéri and Benedek, 2009) (more detailed information is provided in Supplementary Methods).

2.3. Drug protocol

Sprays were prepared by the KU Leuven University Hospital pharmacist. OT (Syntocinon®, Sigma-tau) and placebo (PL) (saline natriumchloride solution) were administered in amber 15 ml glass bottles with metered pump (ACA Pharma). Each puff per nostril contained 4 international units (IU) of OT. In healthy humans, the impact of OT on social cognition is commonly evaluated using a single-dose of intranasal OT, typically given 30–45 min before the experimental task (see Guastella and MacLeod, 2012 for a review). The efficacy of this time interval for intranasal oxytocin administration has been confirmed by animal research (Chang et al., 2012; Neumann et al., 2013) and human research (Daughters et al., 2015). Consequently, also in the present study, a single-dose of 24 IU OT was delivered as 3 puffs per nostril, 30 min before the start of the experimental procedures.

All participants received clear instructions about the use of the nasal spray. At first use, air present in the nasal spray was removed by pumping the spray until a fine mist was observed. Participants were instructed to keep one nostril closed, to take a deep breath through the nose and to tilt their head slightly backwards during nasal administration in order to minimize gravitational loss of the spray. To assure proper use of the spray and to validate tolerability, each subject administered the first dose in front of the experimenter and commented on their experience (e.g. particular smell or taste). All participants were monitored onsite until approximately one hour after nasal spray administration. All participants were screened for potential adverse events or side effects (see Supplementary Table 1 for side effects questionnaire).

2.4. Task and stimuli

A computer-based two-choice emotion recognition task was used as a behavioral measure to assess the effect of a single-dose of OT administration. Participants also performed a two-choice control task matched on motor requirements and task demands, which enables to correct for potential unspecific changes in task performance from the baseline to the post-session (e.g., related to basic differences in task compliance or attention).

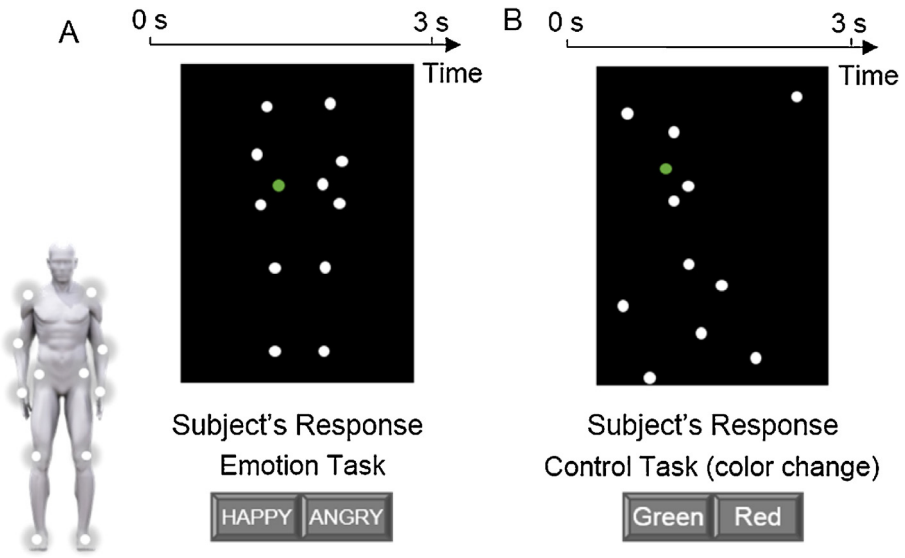

Fig. 1. Participants determined the emotional state or color change of PLDs in which moving white dots reflected the main joints of the human body. (A) During the emotion task, participants were instructed to indicate the emotional state of the moving point light figure (happy or angry). (B) Scrambled versions of the PLD stimuli were presented in a two-choice control task matched on motor requirements and task demands. Here, one of the dots in the PLD briefly changed color to either red or green and participants had to indicate the color change.

The emotion recognition task involved the recognition of 'emotional states' from bodily kinematics as depicted by point light displays (PLDs). The adopted PLD stimuli were based on motion capture data as previously described (Alaerts et al., 2011). In short, all PLDs showed twelve moving white dots against a black background representing the motion of the joints of the ankles, knees, hips, wrists, elbows and shoulders of the human body (Fig. 1). PLD stimuli represent an impoverished but highly controlled form of human motion, representing solely the bodily kinematics without any distracting details on form or background.In the adopted PLD movies (duration 3 s), male and female actors were displayed performing one of three actions (walking, jumping or kicking a ball using the right leg) in either a happy or angry emotional state. All movies were presented from three different viewpoints (front view (0°), side view (90°) and intermediate view (45°) and either in upright or inverted (upside-down) position. As such, the total set of stimuli consisted of 72 movies (2 genders x 3 actions x 2 emotional states x 3 perspectives x 2 positions). At each trial of the emotion recognition task (Supplementary Movie 1), participants were instructed to indicate as accurately and as quickly as possible whether the presented PLD figure was either happy or angry by pressing the respective response buttons (happy or angry) (Fig. 1A). Participants also performed a control 'color' task (Supplementary Movie 2), during which a 'scrambled' version of the PLDs were presented and participants were instructed to indicate color changes in the moving point lights (Fig. 1B). Particularly, for each of the PLD movies used in the emotion recognition task, a scrambled version was created in which the same twelve dots undergo the same local trajectories as in the original PLDs, but with the starting position randomly permutated. In these stimuli, one dot changed color to red or green at a random time point and participants were instructed to indicate as accurately and quickly as possible the color of the dot by pressing the respective response buttons (green or red). Each participant executed the tasks in a quiet room on the same computer monitor. Instructions were provided verbally as well as on the computer monitor at the start of the test. No feedback was provided during the task. Accuracy and reaction times were recorded using E-Prime software (Psychological Software Tools).

2.5. Procedure

To assess the single-dose effect of OT on emotion recognition from PLDs, performance on the emotion task was assessed at baseline and after OT administration. A different set of PLD stimuli was presented before and after OT administration to avoid a repeated presentation (i.e., note that the use of *identical* sets of PLD stimuli before and after nasal spray administration was shown to induce general increases in performance from baseline to post-sessions, reflecting an overall memory effect based on the repeated presentation of stimuli (see Supplementary Fig. 1)). In the current experiment, half of the PLD stimuli were randomly selected to assess emotion recognition performance at baseline and the other half of PLD stimuli was used to assess performance after OT administration. Note that across OT and PL groups, the same set of stimuli was adopted to assess 'baseline' or 'post' performance. At the start of the experimental session participants received verbal instructions on the purpose and procedure of the tasks and completed a short practice of ten trials to familiarize them with the stimuli and task instructions. Performance was then assessed immediately before (baseline measure) and 30 min after (post measure) a single-dose of nasal spray administration (OT or PL).

2.6. Data analysis and statistics

For the emotion and control task, reaction times (RTs) and accuracy rates (percentage correct answers) were calculated to assess performance at the baseline and the post session.

For the emotion recognition task, we also derived the hit rate (h) and false alarm rate (f) to calculate the discrimination sensitivity [d' = z(h)− z(f)] and response bias [criterion = −1/2[z(h) + z(f)]]. For each trial, participants were allowed to indicate their response within a time interval of 4000 milliseconds. Across all participants and trials, a few trials were lost due to 'no recorded response' [Emotion $task_{baseline}$: 3.07%; Emotion $task_{post}$: 1.65%; Control $task_{baseline}$: 0.16%; Control $task_{post}$: 0.47%]. No further trials were discarded based on outlier detection of the RT data (i.e., no RTs exceeded $Q3 \pm 3 \times (Q3–Q1)$ with Q1 and Q3 denoting the first and third quartile over the whole set of trials for each subject) (Electronic Statistics Textbook, StatSoft, Inc. Tulsa).

For all performance measures (RTs, accuracy, discrimination sensitivity, response bias), Shapiro-Wilk's W tests were used to investigate the normality of data distribution. Only for the accuracy scores of the control task, data deviated from the normal distribution. As such, for these data, non-parametric Mann-Whitney U Tests for independent samples (OT, PL) were used to assess treatment-dependent changes in performance from baseline to post. For all other performance measures, repeated-measures Analysis of Variance (ANOVA) were conducted with the between-subject factor 'group' (OT and PL) and the within-subject factor 'time' (baseline, post). Further, to assess the effect size of the OT treatment, Cohen's d (Cohen, 1988) was calculated by subtracting the baseline-to-post change in performance of the PL group from the baseline-to-post performance change of the OT group ((Performance change$_{OT}$ − Performance change$_{PL}$)/sqrt($SD_{OT}\hat{2}$ + $SD_{PL}\hat{2}$)). All statistics were executed with Statistica 10 (StatSoft. Inc. Tulsa, USA). The significance level was set at $p < 0.05$ for all analyses.

3. Results

Performance measures are displayed separately for each treatment group (OT, PL) and session (baseline, post) in Figs. 2 and 3 and in Supplementary Table 2. In Table 1, baseline-to-post performance changes are listed for each treatment group (OT, PL) and corresponding Cohen's d effect sizes are reported (Performance change$_{OT}$ − Performance change$_{PL}$)/pooled SD).

3.1. Accuracy

A repeated-measures ANOVA analysis with the between-subject factor 'group' (OT, PL) and the within-subject factor 'time' (baseline, post) was conducted to explore the effects of OT on performance accuracy of the emotion recognition task. A significant 'group x time' interaction was revealed ($F(1.41) = 5.30$; $p < 0.05$; $\eta^2 = 0.12$; power = 0.61), indicating that performance on the emotion recognition task significantly increased from the baseline to the post session in the OT group (Tukey's HSD test: $p < 0.05$), but not in the PL group (Tukey's HSD test $p = 0.99$) (Fig. 2) (Cohen's d = 0.70, medium effect). Note that baseline performance was not significantly different between treatment groups (Tukey's HSD test $p = 0.56$). Also no main effects of 'group' ($F(1.41) = 0.10$; $p = 0.75$) or 'time' ($F(1.41) = 2.62$; $p = 0.11$) were revealed.

Non-parametric Mann-Whitney U Tests were performed to assess changes in performance accuracy of the control task from the baseline to the post session. As seen in Fig. 2, pre-post changes in basic performance of the control task were tentatively more pronounced in the OT compared to the PL group, but the difference was not significant (Mann-Whitney U: $Z = 1.19$; $p = 0.23$) (Cohen's d = 0.44, small effect).

To directly explore whether treatment-dependent effects on the emotion task were potentially driven by unspecific changes in task performance from the baseline to the post session (e.g., related to session-dependent differences in task compliance or attention), a general linear regression analysis was conducted with performance on the control task as a covariate-of-no-interest. This analysis revealed that the treatment-dependent effect on the emotion task persisted after correction for basic performance changes on the control task ($F(1.40) = 4.84$; $p < 0.05$; $\eta^2 = 0.11$; power = 0.58).

3.2. Reaction times

Repeated-measures ANOVA analysis on the reaction time measures of the emotion task failed to reveal a significant main effect of 'time' ($F(1.41) = 2.26$; $p = 0.14$) or 'group' ($F(1.41) = 0.52$; $p = 0.47$) (Fig. 2). Also no significant 'group x time' interaction effect was revealed ($F(1.41) = 1.08$; $p = 0.30$; $\eta^2 = 0.03$; power = 0.17) indicating that OT did not differentially influence reaction times (Cohen's d = 0.32, small effect).

Also for reaction times on the control task, no significant main effect of 'time' or interaction was revealed (both $F < 2.00$, $p > 0.19$) (Cohen's d = 0.40, small effect). However, on the control task, a main effect of group ($F(1.41) = 4.83$; $p < 0.05$) was revealed, indicating that reaction times were generally lower in the OT group compared to the PL group (Fig. 2).

3.3. Discrimination sensitivity and response bias in emotion recognition

Repeated-measures ANOVA analyses with the between-subject factor 'group' (OT, PL) and the within-subject factor 'time' (baseline, post) were conducted to explore treatment-dependent changes in discrimination sensitivity (d') and response bias (criterion) for indicating the bodily emotional states in the emotion task (happy, angry).

For the discrimination sensitivity index, a significant 'group x time' interaction was revealed ($F(1.41) = 5.00$; $p < 0.05$; $\eta^2 = 0.11$; power = 0.59), indicating that discrimination sensitivity significantly increased from the baseline to the post session in the OT group (Tukey's HSD test: $p < 0.01$), but not in the PL group (Tukey's HSD test $p = 0.99$) (Fig. 3) (Cohen's d = 0.68, medium effect).

In terms of response bias (criterion), no treatment-related effects were observed, indicating that OT treatment did not significantly alter the observers' tendency to label the presented emotional states as e.g. happy or angry ($F(1.41) = 0.45$; $p = 0.50$; $\eta^2 = 0.01$; power = 0.10). Also note that at both sessions (baseline, post) and for each treatment group (OT, PL), criterion scores were not significantly smaller than zero (bias to respond 'happy') or higher than zero (bias to respond 'angry') (all, $p > 0.30$).

3.4. Secondary analyses

Secondary analyses were conducted to verify whether treatment-dependent effects on emotion recognition accuracy were modulated by the type of emotion. To do so, we repeated the 'group x time' ANOVA analysis with 'emotion type' (happy vs. angry) as an additional within-subject factor, forming a three-way 'group' by 'time' by 'emotion type' ANOVA model. This analysis failed to reach significance however ($F(1.41) = 0.61$, $p = 0.44$), indicating that the enhancing effect of OT on emotion recognition was not differentially modulated by the type of the presented emotion.

Further secondary analyses were conducted to verify whether treatment-dependent effects were modulated by (i) the orientation of the presented PLD stimuli (upright, inverted) or (ii) the viewing perspective (front view (0°), side view (90°) and intermediate view (45°)).

For 'orientation', the three-way interaction 'group x time x orientation' was not significant, indicating that the enhancing effect of OT on emotion recognition was not differentially modulated by the orientation of the presented stimuli ($F(1.42) = 0.45$; $p = 0.47$). Note however that a significant main effect of 'orientation' was revealed, indicating that across sessions and treatment groups, performance accuracy was higher for recognizing emotional states from upright, compared to inverted PLD stimuli ($F(1.42) = 95.50$; $p < 0.001$).

For the three-way ANOVA analysis assessing the modulating effect of 'perspective', a significant three-way interaction was revealed ($F(2.84) = 4.64$; $p < 0.05$), indicating that overall, treatment-related effects were more pronounced for side view (90°) and intermediate view (45°) stimuli, compared to front view (0°) stimuli.

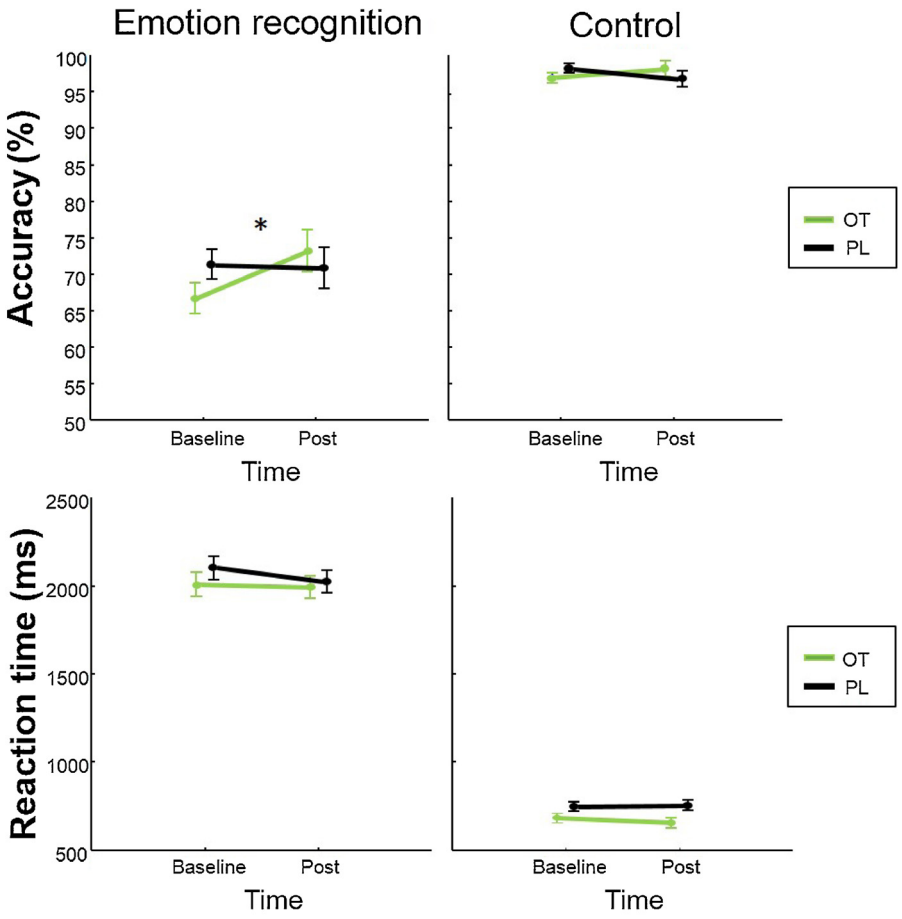

Fig. 2. For each task (emotion recognition, control), accuracy (% correct scores) (upper graphs) and reaction times (lower graphs) are displayed separately for each treatment group (oxytocin (OT); placebo (PL)) and session (baseline, post). Vertical lines denote ± standard error.

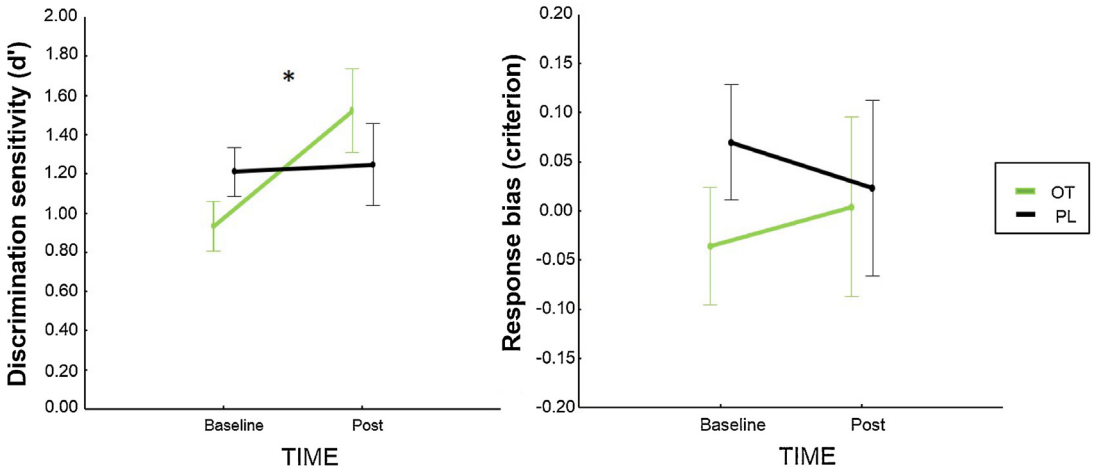

Fig. 3. Discrimination sensitivity (d') and response bias (criterion) for indicating the bodily emotional states in the emotion task (happy, angry) are displayed separately for each treatment group (oxytocin (OT); placebo (PL)) and session (baseline, post). Vertical lines denote ± standard error.

4. Discussion

The current study presents results of a double-blind between-subjects randomized placebo-controlled trial assessing the immediate (single-dose) effects of oxytocin (OT) on reading emotional body language. Overall, a single-dose of OT administration had a significant effect of medium size on emotion recognition, indicating that a single-dose of intranasal OT administration can enhance the reading of other's emotional body language from point light displays. Overall, these findings of OT-induced improvements in bodily emotion recognition from whole-body point light displays in young healthy adults extend previous results assessing the effects of OT on biological motion processing (Kéri and Benedek, 2009; Perry et al., 2010) and the effects of OT on facial emotion recognition (Domes, 2007; Lischke et al., 2012; Marsh et al., 2010; Schulze et al., 2011). A study by Guastella et al. (2008) showed that OT can

Table 1
Change from baseline scores for each treatment group (oxytocin, placebo) and corresponding Cohen's d effect sizes (Performance change$_{OT}$ − Performance change$_{PL}$)/pooled SD).

Outcome measure	Oxytocin	Placebo	
	Change from baseline Mean ± SD	Change from baseline Mean ± SD	Cohen's d
Emotion Recognition Task			
ACC (%)	6.48 ± 10.22	-0.44 ± 9.51	0.70
RT (ms)	-14.41 ± 203.48	-79.34 ± 205.50	0.32
Discrimination Sensitivity (d')	0.59 ± 0.99	0.04 ± 0.60	0.68
Response Bias (criterion)	0.04 ± 0.40	-0.05 ± 0.44	0.21
Control Task			
ACC (%)	1.26 ± 4.65	-1.52 ± 7.45	0.44
RT (ms)	-30.97 ± 96.66	7.35 ± 95.04	0.40

Note. ACC = Accuracy rates in percentages; RT = reaction times for correct answers in milliseconds.

increase the number of fixations and total gaze time toward the eye region of other people. Considering that the eyes represent a salient social cue of the face and a primary source for detection of interpersonal interest, and emotional states of others, the OT-induced enhancement of eye-region processing was suggested as the possible mechanism underlying the positive effects of OT on facial perception and interpersonal communication (Domes, 2007; Gamer et al., 2010). Together with the initial results of Kéri and Benedek (2009), showing an effect of OT on basic biological motion processing, the findings of the present study provide indications that the mechanism by which OT induces prosocial behavior is not restricted to facial cues such as the eye region, but instead generalizes to other sources of socially-relevant information, such as cues originating from the bodily kinematics of others. To date however, the underlying neural mechanism by which OT can enhance the processing of biological motion information is largely unclear. One study by Perry et al. (2010) showed that intranasal OT can significantly enhance the extent of EEG mu suppression over the sensory-motor regions in the brain during the observation of PLD biological motion, which was hypothesized to reflect an enhanced 'mapping' or 'motor resonance' of observed bodily expressions in the 'mirror motor circuitry' of the brain. Social neuroscience is increasingly focusing on the role of the observer's own motor system in understanding or 'reading' other's bodily kinematics (Gallese, 2009, 1998; Gallese et al., 2004; Sinigaglia and Sparaci, 2010). Within the framework of the social-cognitive simulation theory (Carruthers and Smith, 1996; Davies and Stone, 1995) and the ideomotor theory (Prince, 2005), it was posited that the 'understanding of other's actions and behavior' may be essentially motor, rather than sensory in nature. Only recently, De Coster et al. (2014) explored the link between OT and motor simulation of observed actions and showed that intranasal administration of OT can increase automatic imitative behavior, which is supportive of the notion that OT can enhance the mirroring of other's actions.

While OT may act directly on the brain's mirror-motor circuitry to enhance the processing of facial or bodily cues, the possibility cannot be ruled out that the effects of OT on social information processing might be related to more general OT-induced modulations of attention orienting, thereby increasing the saliency of social cues in the observed environment (Shamay-Tsoory and Abu-Akel, 2015). Indeed, while changes in EEG mu-suppression were most evident over the sensorimotor cortex in the study by Perry et al. (2010), responses were not limited to this region, suggesting that also other perceptual and attentional processes are potentially influenced by OT. In support of this notion, several studies showed effects of OT on the orienting of attention in response to emotional gaze cues (Tollenaar et al., 2013) and attentional shifts toward happy facial expressions (Domes et al., 2013). Also more recently, (Xu et al., 2015) showed that OT can improve the allocation of attentional resources towards neutral and positive facial expressions, but not for non-social stimuli or negative facial expressions (Xu et al., 2015). On the other hand, an eye-tracking study of Lischke et al. (2012), failed to show an association between the direction of overt visual attention and OT-induced improvements of facial emotion recognition, and this irrespective of the type of emotional expression. In the present study, our bodily emotion recognition paradigm included two emotional states ('happiness' and 'anger'). While our results indicate that OT can increase the discrimination sensitivity for labeling these emotions, OT-induced improvements in emotion recognition were not differentially modulated by the emotional valence of the presented stimuli (positive versus negative). Also no OT-related changes in response bias were observed, indicating that the overall tendency to label an observed emotional state as 'happy' (positive) or 'angry' (negative) was not changed by the administration of OT. While these explorations on the modulating role of emotional valence are interesting, it should be noted that the effects of OT may not be restricted to the processing of emotional content per se. Particularly, in the study by Kéri and Benedek (2009), point light display stimuli were adopted without emotional content and results showed that the presence of biological motion (versus non-biological motion) was both necessary and sufficient to induce OT-related enhancements in perception (Kéri and Benedek, 2009). In this view, it appears that OT may alter the processing of 'bodily' socially-relevant cues *in general*, but that the social saliency of these cues is not strictly determined by the presence or absence of explicit emotional content. With the present study, we showed that OT can enhance bodily emotion recognition and that the effects were not modulated by the valence of the emotional stimuli. For future experiments, it would however be interesting to directly compare the effects of OT on basic biological motion perception with the effects of OT on the perception of emotional content conveyed by the stimuli. Such designs would allow disentangling whether the additional presence of emotional content potentially increased the perceived social saliency of the presented cue, or whether the mere presence of a biological actor is equally salient to evaluate the presented stimulus as socially relevant.

Several functional neuroimaging studies from our (Alaerts et al., 2014) and other labs (Bolling et al., 2013; Pelphrey et al., 2005; Vander Wyk et al., 2012), as well as TMS/tDCS brain stimulation studies (Avenanti et al., 2013; Grossman et al., 2005; van Kemenade et al., 2012; Vonck et al., 2015) and lesion studies (Saygin, 2007) highlighted the importance of a cortical area in the superior temporal sulcus (STS) in biological motion processing. Also beyond biological motion detection, the STS has been shown to play an important role in several other social cognitive functions, including face perception, speech processing, directing of eye gaze and mentalization (Carrington and Bailey, 2009; Redcay, 2008). Overall, the STS is known to form an integral part of the brain's neural circuitry underlying social cognition, including the amygdala-orbitofrontal

social brain, and also in relation to the human fronto-parietal mirror motor system, the STS has been hypothesized to form the main visual input area (Iacoboni et al., 2001). In the context of OT, results from a recent meta-analysis of human neuroimaging studies exploring the neural effects of single-dose OT administration specifically identified changes in brain activity in temporal areas including the STS as well as the insula during the processing of social stimuli (Wigton et al., 2015). Together, these findings highlight the STS as a possible neural target by which OT can exert increasing effects on bodily emotion recognition, either by directly modulating the processing within this region, or indirectly by altering its connected neural circuitry. Future research is necessary however to further unravel the exact neural basis by which OT can mediate the processing of biological motion and bodily emotional expressions. Considering earlier reports on difficulties of patients with autism spectrum disorders (ASD) with the processing of biological motion (Kaiser and Pelphrey, 2012; Nackaerts et al., 2012) and emotion recognition more general (for review see Harms et al., 2010), these insights will be important to further evaluate the potential of OT as a novel treatment for ASD. In the present study, only healthy neurotypical males were included to assess the single-dose effects of OT administration on bodily emotion recognition and overall, the revealed effects were moderate. It would therefore be interesting for future studies to explore whether the present effects can be replicated or even enlarged in populations with particular deficits in the social domain, such as ASD.

Role of the funding sources

This research was supported by grants from the Flanders Fund for Scientific Research (FWO projects KAN 1506716N, KAN 1521313N, & G.0401.12) and the Branco Weiss fellowship of the Society in Science – ETH Zurich granted to K.A. S.B. is supported by a fund of the Marguerite-Marie Delacroix foundation.

Conflict of interests

The authors declare no conflict of interest.

Acknowledgements

We are thankful to all the participating subjects and Stephanie Brams for assistance with the data collection.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.psyneuen.2016.07.002.

References

Alaerts, K., Nackaerts, E., Meyns, P., Swinnen, S.P., Wenderoth, N., 2011. Action and emotion recognition from point light displays: an investigation of gender differences. PLoS One 6, e20989, http://dx.doi.org/10.1371/journal.pone.0020989.

Alaerts, K., Woolley, D.G., Steyaert, J., Di Martino, A., Swinnen, S.P., Wenderoth, N., 2014. Underconnectivity of the superior temporal sulcus predicts emotion recognition deficits in autism. Soc. Cogn. Affect. Neurosci. 9, 1589–1600, http://dx.doi.org/10.1093/scan/nst156.

Auyeung, B., Lombardo V, M., Heinrichs, M., Chakrabarti, B., Sule, A., Deakin, J.B., Bethlehem, R.A.I., Dickens, L., Mooney, N., Sipple, J.A.N., Thiemann, P., Baron-Cohen, S., 2015. Oxytocin increases eye contact during a real-time, naturalistic social interaction in males with and without autism. Transl. Psychiatry 5, e507, http://dx.doi.org/10.1038/tp.2014.146.

Avenanti, A., Annella, L., Candidi, M., Urgesi, C., Aglioti, S.M., 2013. Compensatory plasticity in the action observation network: virtual lesions of STS enhance anticipatory simulation of seen actions. Cereb. Cortex 23, 570–580, http://dx.doi.org/10.1093/cercor/bhs040.

Bolling, D.Z., Pelphrey, K.A., Kaiser, M.D., 2013. Social inclusion enhances biological motion processing: a functional near-infrared spectroscopy study. Brain Topogr. 26, 315–325, http://dx.doi.org/10.1007/s10548-012-0253-y.

Bos, P.A., Montoya, E.R., Hermans, E.J., Keysers, C., van Honk, J., 2015. Oxytocin reduces neural activity in the pain circuitry when seeing pain in others. Neuroimage 113, 217–224, http://dx.doi.org/10.1016/j.neuroimage.2015.03.049.

Carrington, S.J., Bailey, A.J., 2009. Are there theory of mind regions in the brain? A review of the neuroimaging literature. Hum. Brain Mapp. 30, 2313–2335, http://dx.doi.org/10.1002/hbm.20671.

Carruthers, P., Smith, P., 1996. Theories of Theories of Mind. Cambridge University Press, Cambridge.

Chang, S.W.C., Barter, J.W., Ebitz, R.B., Watson, K.K., Platt, M.L., 2012. Inhaled oxytocin amplifies both vicarious reinforcement and self reinforcement in rhesus macaques (Macaca mulatta). Proc. Natl. Acad. Sci. U. S. A. 109, 959–964, http://dx.doi.org/10.1073/pnas.1114621109.

Cohen, J., 1988. Statistical Power Analysis for the Behavioral Sciences, 2nd ed. Lawrence Erlbaum Associates, New Jersey.

Daughters, K., Manstead, A.S.R., Hubble, K., Rees, A., Thapar, A., van Goozen, S.H.M., 2015. Salivary oxytocin concentrations in males following intranasal administration of oxytocin: a double-blind, cross-over study. PLoS One 10, e0145104, http://dx.doi.org/10.1371/journal.pone.0145104.

Davies, M., Stone, T., 1995. Mental Simulation: Evaluations and Applications. Blackwell Publishers, Oxford.

De Coster, L., Mueller, S.C., T'sjoen, G., De Saedeleer, L., Brass, M., 2014. The influence of oxytocin on automatic motor simulation. Psychoneuroendocrinology 50, 220–226, http://dx.doi.org/10.1016/j.psyneuen.2014.08.021.

Domes, G., Sibold, M., Schulze, L., Lischke, A., Herpertz, S.C., Heinrichs, M., 2013. Intranasal oxytocin increases covert attention to positive social cues. Psychol. Med. 43, 1747–1753, http://dx.doi.org/10.1017/S0033291712002565.

Domes, G., Heinrichs, M., Michel, A., Berger, C., Herpertz, S.C., 2007. Oxytocin improves mind-reading in humans. Biol. Psychiatry 61, 731–733, http://dx.doi.org/10.1016/j.biopsych.2006.07.015.

Galbally, M., Lewis, A.J., Ijzendoorn, M., van Permezel, M., 2011. The role of oxytocin in mother-infant relations: a systematic review of human studies. Harv. Rev. Psychiatry 19, 1–14, http://dx.doi.org/10.3109/10673229.2011.549771.

Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends Cogn. Sci. 8, 396–403, http://dx.doi.org/10.1016/j.tics.2004.07.002.

Gallese, V., 1998. Mirror neurons and the simulation theory of mind-reading. Trends Cogn. Sci. 2, 493–501, http://dx.doi.org/10.1016/S1364-6613(98)01262-5.

Gallese, V., 2009. Mirror neurons embodied simulation, and the neural basis of social identification. Psychoanal. Dialogues 19, 519–536, http://dx.doi.org/10.1080/10481880903231910.

Gamer, M., Zurowski, B., Büchel, C., 2010. Different amygdala subregions mediate valence-related and attentional effects of oxytocin in humans. Proc. Natl. Acad. Sci. U. S. A. 107, 9400–9405, http://dx.doi.org/10.1073/pnas.1000985107.

Grossman, E.D., Battelli, L., Pascual-Leone, A., 2005. Repetitive TMS over posterior STS disrupts perception of biological motion. Vision Res. 45, 2847–2853, http://dx.doi.org/10.1016/j.visres.2005.05.027.

Guastella, A.J., MacLeod, C., 2012. A critical review of the influence of oxytocin nasal spray on social cognition in humans: evidence and future directions. Hormones Behav. 61, 410–418, http://dx.doi.org/10.1016/j.yhbeh.2012.01.002.

Guastella, A.J., Mitchell, P.B., Dadds, M.R., 2008. Oxytocin increases gaze to the eye region of human faces. Biol. Psychiatry 63, 3–5, http://dx.doi.org/10.1016/j.biopsych.2007.06.026.

Harms, M.B., Martin, A., Wallace, G.L., 2010. Facial emotion recognition in autism spectrum disorders: a review of behavioral and neuroimaging studies. Neuropsychol. Rev. 20, 290–322, http://dx.doi.org/10.1007/s11065-010-9138-6.

Hurlemann, R., Scheele, D., 2015. Dissecting the role of oxytocin in the formation and loss of social relationships. Biol. Psychiatry 79, 185–193, http://dx.doi.org/10.1016/j.biopsych.2015.05.013.

Iacoboni, M., Koski, L.M., Brass, M., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C., Rizzolatti, G., 2001. Reafferent copies of imitated actions in the right superior temporal cortex. Proc. Natl. Acad. Sci. U. S. A. 98, 13995–13999, http://dx.doi.org/10.1073/pnas.241474598.

Insel, T.R., 2010. The challenge of translation in social neuroscience: a review of oxytocin, vasopressin, and affiliative behavior. Neuron 65, 768–779, http://dx.doi.org/10.1016/j.neuron.2010.03.005.

Kéri, S., Benedek, G., 2009. Oxytocin enhances the perception of biological motion in humans. Cogn. Affect. Behav. Neurosci. 9, 237–241, http://dx.doi.org/10.3758/CABN.9.3.237.

Kaiser, M.D., Pelphrey, K.a., 2012. Disrupted action perception in autism: behavioral evidence, neuroendophenotypes, and diagnostic utility. Dev. Cogn. Neurosci. 2, 25–35, http://dx.doi.org/10.1016/j.dcn.2011.05.005.

Kendrick, K.M., 2000. Oxytocin, motherhood and bonding. Exp. Physiol. 85, 111s–124s, http://dx.doi.org/10.1111/j.1469-445X.2000.tb00014.x.

Lischke, A., Berger, C., Prehn, K., Heinrichs, M., Herpertz, S.C., Domes, G., 2012. Intranasal oxytocin enhances emotion recognition from dynamic facial expressions and leaves eye-gaze unaffected. Psychoneuroendocrinology 37, 475–481, http://dx.doi.org/10.1016/j.psyneuen.2011.07.015.

Marsh, A.A., Yu, H.H., Pine, D.S., Blair, R.J.R., 2010. Oxytocin improves specific recognition of positive facial expressions – ProQuest. Psychopharmacology (Berl.) 209, 225–232.
Nackaerts, E., Wagemans, J., Helsen, W., Swinnen, S.P., Wenderoth, N., Alaerts, K., 2012. Recognizing biological motion and emotions from point-light displays in autism spectrum disorders. PLoS One 7, 1–12, http://dx.doi.org/10.1371/journal.pone.0044473.
Nave, G., Camerer, C., McCullough, M., 2015. Does oxytocin increase trust in humans? A critical review of research. Perspect. Psychol. Sci. 10, 772–789, http://dx.doi.org/10.1177/1745691615600138.
Neumann, I.D., Maloumby, R., Beiderbeck, D.I., Lukas, M., Landgraf, R., 2013. Increased brain and plasma oxytocin after nasal and peripheral administration in rats and mice. Psychoneuroendocrinology 38, 1985–1993, http://dx.doi.org/10.1016/j.psyneuen.2013.03.003.
Pelphrey, K.A., Morris, J.P., Michelich, C.R., Allison, T., McCarthy, G., 2005. Functional anatomy of biological motion perception in posterior temporal cortex: an FMRI study of eye, mouth and hand movements. Cereb. Cortex 15, 1866–1876, http://dx.doi.org/10.1093/cercor/bhi064.
Perry, A., Bentin, S., Shalev, I., Israel, S., Uzefovsky, F., Bar-On, D., Ebstein, R.P., 2010. Intranasal oxytocin modulates EEG mu/alpha and beta rhythms during perception of biological motion. Psychoneuroendocrinology 35, 1446–1453, http://dx.doi.org/10.1016/j.psyneuen.2010.04.011.
Prince, W., 2005. An ideomotor approach to imitation. In: Hurley, S., Chater, N. (Eds.), Perspective on Imitation. MIT Press55 Hayward Street, Cambridge, MA Cambridge, pp. 141–156.
Redcay, E., 2008. The superior temporal sulcus performs a common function for social and speech perception: implications for the emergence of autism. Neurosci. Biobehav. Rev. 32, 123–142, http://dx.doi.org/10.1016/j.neubiorev.2007.06.004.
Saygin, A.P., 2007. Superior temporal and premotor brain areas necessary for biological motion perception. Brain 130, 2452–2461, http://dx.doi.org/10.1093/brain/awm162.
Schulze, L., Lischke, A., Greif, J., Herpertz, S.C., Heinrichs, M., Domes, G., 2011. Oxytocin increases recognition of masked emotional faces. Psychoneuroendocrinology 36, 1378–1382, http://dx.doi.org/10.1016/j.psyneuen.2011.03.011.
Shamay-Tsoory, S.G., Abu-Akel, A., 2015. The social salience hypothesis of oxytocin. Biol. Psychiatry 79, 194–202, http://dx.doi.org/10.1016/j.biopsych.2015.07.020.
Sinigaglia, C., Sparaci, L., 2010. Emotions in action through the looking glass1. J. Anal. Psychol. 55, 3–29, http://dx.doi.org/10.1111/j.1468-5922.2009.01821.x.
Strauss, G.P., Keller, W.R., Koenig, J.I., Sullivan, S.K., Gold, J.M., Buchanan, R.W., 2015. Endogenous oxytocin levels are associated with the perception of emotion in dynamic body expressions in schizophrenia. Schizophr. Res. 162, 52–56, http://dx.doi.org/10.1016/j.schres.2015.01.022.
Sue Carter, C., 1998. Neuroendocrine perspectives on social attachment and love. Psychoneuroendocrinology 23, 779–818, http://dx.doi.org/10.1016/S0306-4530(98)00055-9.
Tollenaar, M.S., Chatzimanoli, M., van der Wee, N.J.A., Putman, P., 2013. Enhanced orienting of attention in response to emotional gaze cues after oxytocin administration in healthy young men. Psychoneuroendocrinology 38, 1797–1802, http://dx.doi.org/10.1016/j.psyneuen.2013.02.018.
Troje, N.F., Westhoff, C., 2006. The inversion effect in biological motion perception: evidence for a life detector? Curr. Biol. 16, 821–824, http://dx.doi.org/10.1016/j.cub.2006.03.022.
Vander Wyk, B.C., Voos, A., Pelphrey, K.A., 2012. Action representation in the superior temporal sulcus in children and adults: an fMRI study. Dev. Cogn. Neurosci. 2, 409–416, http://dx.doi.org/10.1016/j.dcn.2012.04.004.
Vonck, S., Swinnen, S.P., Wenderoth, N., Alaerts, K., 2015. Effects of transcranial direct current stimulation on the recognition of bodily emotions from point-light displays. Front. Hum. Neurosci. 9, 438, http://dx.doi.org/10.3389/fnhum.2015.00438.
Wigton, R., Radua, J., Allen, P., Averbeck, B., Meyer-Lindenberg, A., McGuire, P.K., Shergill, S.S., Fusar-Poli, P., 2015. Neurophysiological effects of acute oxytocin administration: systematic review and meta-analysis of placebo-controlled imaging studies. J. Psychiatry Neurosci. 40, E1–22, http://dx.doi.org/10.1503/jpn.130289.
Xu, L., Ma, X., Zhao, W., Luo, L., Yao, S., Kendrick, K.M., 2015. Oxytocin enhances attentional bias for neutral and positive expression faces in individuals with higher autistic traits. Psychoneuroendocrinology 62, 352–358, http://dx.doi.org/10.1016/j.psyneuen.2015.09.002.
van Kemenade, B.M., Muggleton, N., Walsh, V., Saygin, A.P., 2012. Effects of TMS over premotor and superior temporal cortices on biological motion perception. J. Cogn. Neurosci. 24, 896–904, http://dx.doi.org/10.1162/jocn_a_00194.